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JAW MUSCULATURE OF THE WEST INDIAN SNAKE *ALSOPHIS CANTHERIGERUS BROOKSI* (COLUBRIDAE, REPTILIA).

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ABSTRACT

The West Indian colubrid snake *Alsophis cantherigerus brooksi* is presently assigned to the subfamily Xenodontinae (*sensu* Maglio, 1970). It is a member of an assemblage of related snakes from continental stocks that have spread to and diversified within this Caribbean archipelago. The head myology proves to be representative of other xenodontine snakes of the West Indies and thus is a convenient reference for comparison to other subspecies and may be useful in later comparisons to other species' assemblages of the region. Its jaw musculature conforms basically to that of other generalized colubrid snakes. Special attention is given to the internal fascicular bundles within each muscle.

The adductor mandibulae externus superficialis passes posteroventrally from its origin on the skull, inserting mostly by a broad aponeurosis except, for a rostral slip that forms its anterior edge and inserts directly on the mandible. The adductor mandibulae externus profundus consists of anterior and posterior wedges of muscle delineated by a vertical suture between them. Adductor mandibulae externus medialis is separable into superficial and deep slips. One significant difference in general muscle anatomy from some other colubrids concerns the protractor quadrati. This muscle inserts on the retroarticular process of the mandible which differs from the genus *Opheodrys* in which it is reported to insert on the quadrate.

Lateral jaw musculature proves to be very similar within the subspecies of *Alsophis cantherigerus*. The only detectable difference occurs in the deep division of the depressor mandibulae. In most subspecies (*adspersus, brooksi, cantherigerus, caymanus, schwartzi*), this deep division is a single slip of the depressor arising from a single site. However, in *fuscicauda, pepei,* and *ruttyi* it splits lengthwise so as to arise from two sites of origin. One instance of individual asymmetry was identified in *adspersus* wherein the insertion of the superficialis differs on left and right sides.

The conformity of lateral jaw musculature among subspecies related to *brooksi* emphasizes the uniform nature of this group. Other authors also found this uniformity in features of the integument, skull osteology, and hemipenial characteristics.

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INTRODUCTION

Examination of the West Indian colubrid snakes of the subfamily Xenodontinae by Maglio (1970) served to emphasize the special island biogeographic features of these species. Compared to continental species, West Indian insular members of this subfamily have well delineated distributions and their probable origin, namely from mainland genera, seems better established. Routes of initial colonization by and diversification within the different species assemblages through this Caribbean archipelago were proposed by Maglio as well. With a view to testing this and related proposals on the phylogeny of this group, I examined the jaw musculature of members from the various assemblages, following any changes through the various species on the different islands. This work and its implications will be the subject of later reports. The present paper is restricted to the species *Alsophis cantherigerus* and, in particular, the subspecies *A. c. brooksi.*

This subspecies is found only on the Swan Islands, located almost 200 kilometers north of Honduras. It deserves special attention for several reasons. It is part of the assemblage of closely related populations that spread to and diversified over the islands. Its jaw musculature is representative of the condition in other West Indian xenodontine species. Its jaw anatomy can thus serve as a central point of reference in later analysis of these island snake species. It is also a rare subspecies even in museum collections.

MATERIALS AND METHODS

All descriptions of the head anatomy of *Alosphis cantherigerus brooksi* are based on a single alcohol preserved female specimen from the Museum of Comparative Zoology (MCZ) 11979. The specimen, taken on Swan Islands and donated to the collection in 1916, measured 85.5 cm snout-vent length. The tail, missing its severed tip, measured 23.4 cm. The cranial musculature was exposed initially by cutting through the integument along the lips and reflecting the skin backwards. This revealed that the specimen had sustained a deep cut in the neck musculature that also severed the vertebral column through the fourth cervical vertebra and consequently limited the description of structures in the immediate vicinity. This study centered upon the jaw musculature and therefore often required the disruption of nerves to first confirm muscle at-

tachments with certainty. As a result, some of the peripheral distributions of the nerves were lost before they could be traced with confidence. The blood vessels proved impractical to follow for the same reasons. Consequently, only those pathways and distributions of nerves and blood vessels that could later be confirmed are included in the descriptions. No bilateral asymmetry in jaw musculature was detected. Muscle and ligament terminology follows Haas (1973), Kardong (1973, 1974), and Pregill (1977); interpretation of cranial nerves relies upon Auen and Langebartel (1977); and cephalic gland nomenclature is based on Taub (1966). One departure in nomenclature concerns the muscle running between the neck and dorsal end of the quadrate, which is often referred to as *M. retractor quadrati* especially in descriptions of venomous snakes (e.g. Dullemeijer, 1956). Others employ this same term for a quite different muscle (e.g. Kochva, 1962). To avoid confusion herein, the term *M. cervicoquadratus* is used instead.

The other subspecies of *Alsophis cantherigerus* examined include: *adspersus* (MCZ 68727), *cantherigerus* (MCZ 13288), *caymanus* (MCZ 44886), *fuscicauda* (MCZ 44875), *pepei* (MCZ 13289), *ruttyi* (MCZ 44877), and *schwartzi* (MCZ 56430).

GENERAL DESCRIPTION

Cephalic Glands

The **nasal glands**, like other lateral cephalic glands, are bilaterally paired. Each rests in an anterior depression on the anteromedial face of the prefrontal and is bounded medially by a dorsal process of the respective septomaxilla and by the nasal capsule. The **Harderian gland** (Figs. 2, 3a, 4b) is found ventral to and extends behind the eye. Beneath the eye the gland lies within the orbit and is compressed between eyeball and the ligamentum orbitale interioris (septum interorbitale of Dullemeijer, 1956) which forms the ventral floor of the orbit. Passing posteriorly out of the orbit it enlarges, occupying the space lateral to the levator pterygoidei muscle and medial to the postorbital bone and the adductor mandibulae externus superficialis muscle. The **infralabial glands** (Fig. 4c) extend posteriorly along the lateral aspect of the dentary and compound bones to approximately the level of the anterior insertion of the adductor mandibulae externus superficialis muscle. The **supralabial glands**

extend posteriorly slightly farther. However, they lie along the upper lips and pass lateral to the superficialis muscles and maxillae. Pressed into the side of each supralabial gland and residing behind the eye is the large **Duvernoy's gland** (Fig. 4c), which in the preserved state appears lighter in color and more distinctly lobed. The small, unpaired **premaxillary gland** lies beneath the upper lip on the superficial face of the premaxillary bone.

In the chin, the **sublingual gland** (Fig. 6a, b) is represented by three parts, a single medial and paired lateral glands. The medial sublingual gland is stationed along the ventroanterior end of the tongue and anchored to its connective tissue sheath. The lateral sublingual glands insert into the oral epithelium and serve as attachment sites for the pars glandularis of the transversus branchialis and the protractor larygeus muscles.

Ligaments

A number of small, unnamed ligaments link the cranial elements together, but only the prominent or most commonly cited in the literature are discussed here. Two primary ligaments serve to check the motion of the supratemporal relative to the braincase. One is the **parieto-supratemporal ligament** that runs from the dorsal edge of the supratemporal to the dorsal surface of the exoccipital. It also serves as the site of origin for parts of the adductor mandibulae externus medialis and depressor mandibulae muscles. The other is the **prooto-supratemporal ligament** that attaches to the ventral edge of the supratemporal and to the adjacent region of the braincase. Rotation of the prefrontal is controlled in part by the **fronto-prefrontal ligament** (Fig. 2) from the ventromedial corner of the prefrontal to the adjacent parasphenoid.

Several prominent ligaments are associated with the palato-maxillary arch (pterygoid, ectopterygoid, maxilla, and palatine). Within the arch, the **intramaxillary ligament** (Fig. 2) reaches from the medial ectopterygoid process of the maxilla forward to attach jointly on the palatine process of the maxilla and maxillary process of the palatine. The short, fan-shaped **quadrato-pterygoid ligament** runs from the narrow posterior end of the pterygoid to a wider medial attachment site along the mandible that includes the retroarticular process and extends below the articular notch. The strong, cord-like **maxillo-postorbital ligament** (Fig. 4) reaches from the

downward directed tip of the postorbital to the lateral side of the maxilla just anterior to its articulation with the ectopterygoid. The **quadrato-maxillary ligament** (Fig. 4) begins along the laterodorsal edge of the retroarticular process, passes forward above the lateral condyle of the quadrate, and divides. The smaller division attaches to the nearby dermis beneath the most posterior supralabial scale, whereas the larger division continues forward to attach to the posterolateral region of the maxilla.

Cranial Nerves
Figs. 2, 3a–d, 4a–c

Trigeminal Nerve (V). The trigeminal is one of three major nerves supplying the jaw musculature. Trigeminal branches that supply the jaw musculature exit from the cranium through two openings in the prootic bone, the maxillary and mandibular foramina. Five branches could be found passing through the maxillary foramen. The largest, the maxillary division (V_2), passes lateral to the pseudotemporalis then bends forward continuing in an anterior path dorsal to the origin of the pterygoideus. A second nerve divides lateral to the pseudotemporalis with one branch passing laterally to glandular tissue along the upper lip and the second swinging dorsally, superficial to the facial vein, to enter the ventral surface of the adductor mandibulae externus superficialis. Two other nerves also course dorsally after exiting from the foramen. Both pass deep to the facial vein, but one enters the medial face of the adductor mandibulae externus medialis (deep division) and the other enters the medial face of the adductor mandibulae externus superficialis. The fifth nerve leaving this foramen passes laterally.

Through the mandibular foramen exit six branches of the trigeminal nerve. The largest branch is the mandibular division (V_3) that passes posteriorly and then turns ventrally following a route that carries it between the adductor mandibulae externus profundus and the adductor mandibulae posterior. Eventually it enters a foramen in the mandible located at the anterior end of the mandibular fossa. A second branch of the trigeminal courses posteriorly, then swings dorsally, bifurcates, and enters the medial face of the adductor mandibulae externus profundus and medioposterior face of the adductor mandibulae externus medialis (superficial division). A third nerve passes posteriorly deep to the mandibular division. It sends

one branch between medial and lateral divisions of the adductor mandibulae posterior, another between the pars minimus and the lateral division of adductor mandibulae posterior, and several branches into the medial surface of the adductor mandibulae externus profundus. The remaining three nerves of the trigeminal that exit through the mandibular foramen pass ventrally—one disappears between the pterygoideus and the levator pterygoidei, one enters the lateral face of the pseudotemporalis, and the last runs laterally into the glandular tissue along the upper lip.

Facial Nerve (VII). Two divisions of the facial nerve exit through the mandibular foramen. The larger is the hyomandibular nerve that passes posteriorly over the columella, under the quadrate, and enters the depressor mandibulae. A slender communication arising from the base of the hyomandibular travels posteriorly and merges with craniocervical trunk. The second division of the facial nerve is the palatine nerve. It courses ventrally along the underside of the braincase, is joined by the cranial sympathetic nerve, and then enters the posterior Vidian canal in the ventral aspect of the basisphenoid bone.

Craniocervical Trunk. The glossopharyngeal (IX), vagus (X), and hypoglossal (XII) cranial nerves combine to form a single large nerve or plexus, the craniocervical trunk (Auen and Lagebartel, 1977). In addition, a slender communication runs between the base of the hyomandibular and this trunk. Finally, a spinal nerve (presumably the ventral ramus of the first spinal nerve) emerges from between the rectus capitus anterior pars dorsalis and longissimus dorsi (ventral head) cervical muscles to join with the craniocervical trunk. The trunk sweeps around the side of the body at about the angle of the jaws and supplies various members of the hypobranchial musculature.

Lateral Jaw Musculature

M. cervicomandibularis (cm)
Figs. 1, 4c

The epimysium of the spinalis-semispinalis complex near the dorsal midline serves as the surface of origin. This origin extends along a line even with neural spines 3 to 8 in the nape of the neck and

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Figs. 1, 4c

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partially overlaps the anterior origin of the neuromandibularis. This broad muscle travels ventrally, passing over the deep cervicoquadratus, and narrows abruptly to insert on the lateral epicondyle of the quadrate and on the adjacent part of quadrato-maxillary (dermal) ligament, which passes posteriorly to its own attachment on the dorsolateral retroarticular process.

M. depressor mandibulae (dm)
(M. occipito-quadrato-mandibularis)
Figs. 1, 4 a–c

There are two parts of this muscle, superficial and deep, divided by the cervicoquadratus that passes between these two parts en route to its own insertion. Branches of cranial nerve VII also pass through the belly of the deep division, then along the medial side of the superficial division.

The superficial division has an origin that runs from the parieto-supratemporal ligament next to the adductor mandibulae externus medialis, across the supratemporal to the anterodorsal corner of the quadrate, and extends down along the surface epimysium of adductor mandibulae externus profundus near its own origin. It inserts directly on the lateral rim of the mandibular retroarticular process, overlapping the attachment site of the quadrato-maxillary ligament.

The deep division arises from the posterior tip of the supratemporal and the posterior, dorsomedial edge of the quadrate. It is a parallel muscle that inserts on the dorsomedial surface of the retroarticular process.

M. cervicoquadratus (cq)
Figs. 1, 4 a–c

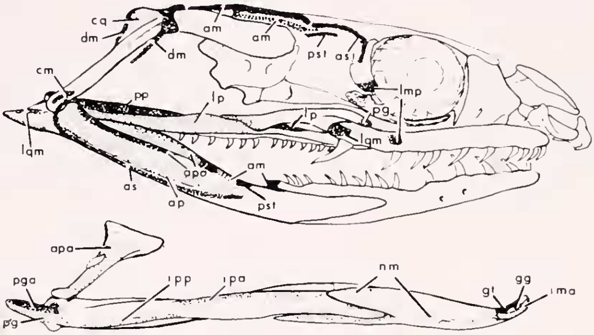
This is a long, tapering muscle that takes origin in the dermis of the lateral integument posterior to the belly of the neuromandibularis over the intercostal muscles. It gradually narrows as it courses forward, slipping under the more superficial cervicomandibularis, becoming a cord-like tendon that passes between the superficial and the deep divisions of the depressor mandibulae to insert laterally on the proximal end of the quadrate just below its posterior corner.

Figure 1. Lateral view of the skull and ventral view of the quadrate and lower jaw showing sites of muscle attachments.

Figure 2. Ventral view of head. The bones of the left palato-maxillary arch have been removed to expose deep structures. On the right, the M. pterygoideus (pg) has been cut and partially reflected and the mandible rotated outward to better expose some of the underlying structures.

Abbreviations:

am	M. adductor mandibulae externus medialis
ap	M. adductor mandibulae externus profundus
apo	M. adductor mandibulae posterior
as	M. adductor mandibulae externus superficialis
br	transverse ridge on basisphenoid
c	columella
cm	M. cervicomandibularis
cp	choanal process of palatine
cq	M. cervicoquadratus
ct	craniocervical nerve trunk (IX, X, XII)
dm	M. depressor mandibulae
gg	M. genioglossus
gt	M. geniotrachealis
Hd	Harderian gland
ima	M. intermandibularis anterior
ipa	M. intermandibularis posterior, pars anterior
ipp	M. intermandibular posterior, pars posterior
lfp	ligamentum fronto-prefrontale
lim	ligamentum intramaxillare
lmp	ligmentum maxillo-postorbitale
loi	ligamentum orbitale inferioris
lp	M. levator pterygoidei
lqm	ligamentum quadrato-maxillare
nm	M. neuromandibularis
pg	M. pterygoideus
pga	M. pterygoideus accessorius
pp	M. protractor pterygoidei
pq	M. protractor quadrati
pst	M. pseudotemporalis
rcd	M. rectus capitus anterior, pars dorsalis
rcv	M. rectus capitus anterior, pars ventralis
rp	M. retractor pterygoidei
rv	M. retractor vomeris
V_2	Trigeminal nerve, maxillary division
V_3	Trigeminal nerve, mandibular division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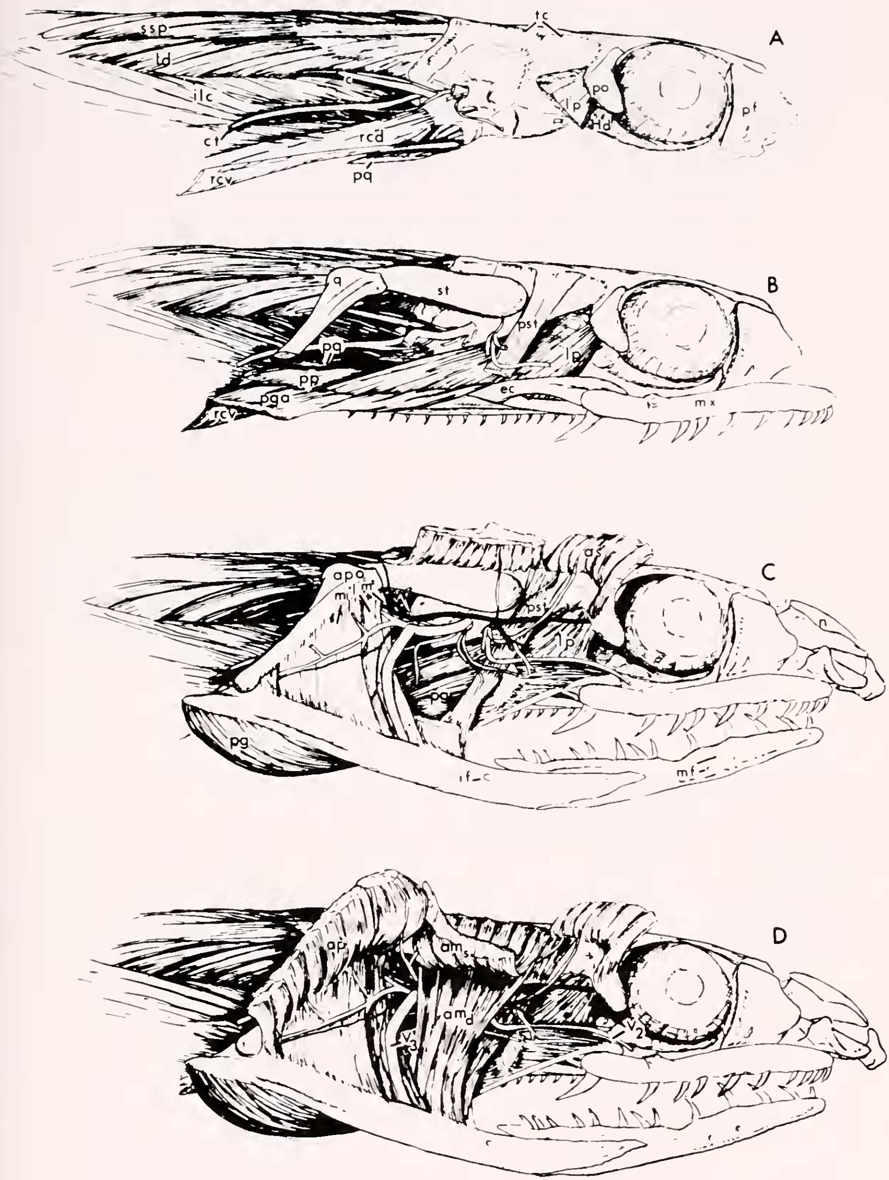
M. adductor mandibulae externus superficialis (as)
Figs, 1, 3 c–d, 4 a–c

A temporal crest, prominent posteriorly, becomes lower as it passes forward along the dorsolateral side of the skull. Anteriorly it curves outward to terminate on the postorbital process of the parietal. The superficialis originates directly from the anterior half of this temporal crest and from the base of the postorbital bone. It passes posteriorly and downward, partially overlying the adductor mandi-

Figure 3. Lateral view of head showing progressively more structures (A–D) in place.

Abbreviations:

am	M. adductor mandibulae externus medialis, deep (d) and superficial (s) divisions
ap	M. adductor mandibulae externus profundus
apo	M. adductor mandibulae posterior, lateral division (l), medial division (m), pars minimus (mi)
as	M. adductor mandibulae externus superficialis
c	columella
ct	craniocervical nerve trunk (IX, X, XII)
ec	ectopterygoid
f	frontal
Hd	Harderian gland
if	infralabial nerve foramen (posterior)
ilc	M. iliocostalis
ld	M. longissimus dorsi
lp	M. levator pterygoidei
mf	mental foramen
mx	maxilla
n	nasal
pf	prefrontal
pg	M. pterygoideus
pga	M. pterygoideus accessorius
po	postorbital
pp	M. protractor pterygoidei
pq	M. protractor quadrati
pst	M. pseudotemporalis
q	quadrate
rcv	M. rectus capitus anterior, pars ventralis
ssp	M. spinalis-semispinalis
st	supratemporal
tc	temporal crest
V_2	Trigeminal nerve, maxillary division
V_3	Trigeminal nerve, mandibular division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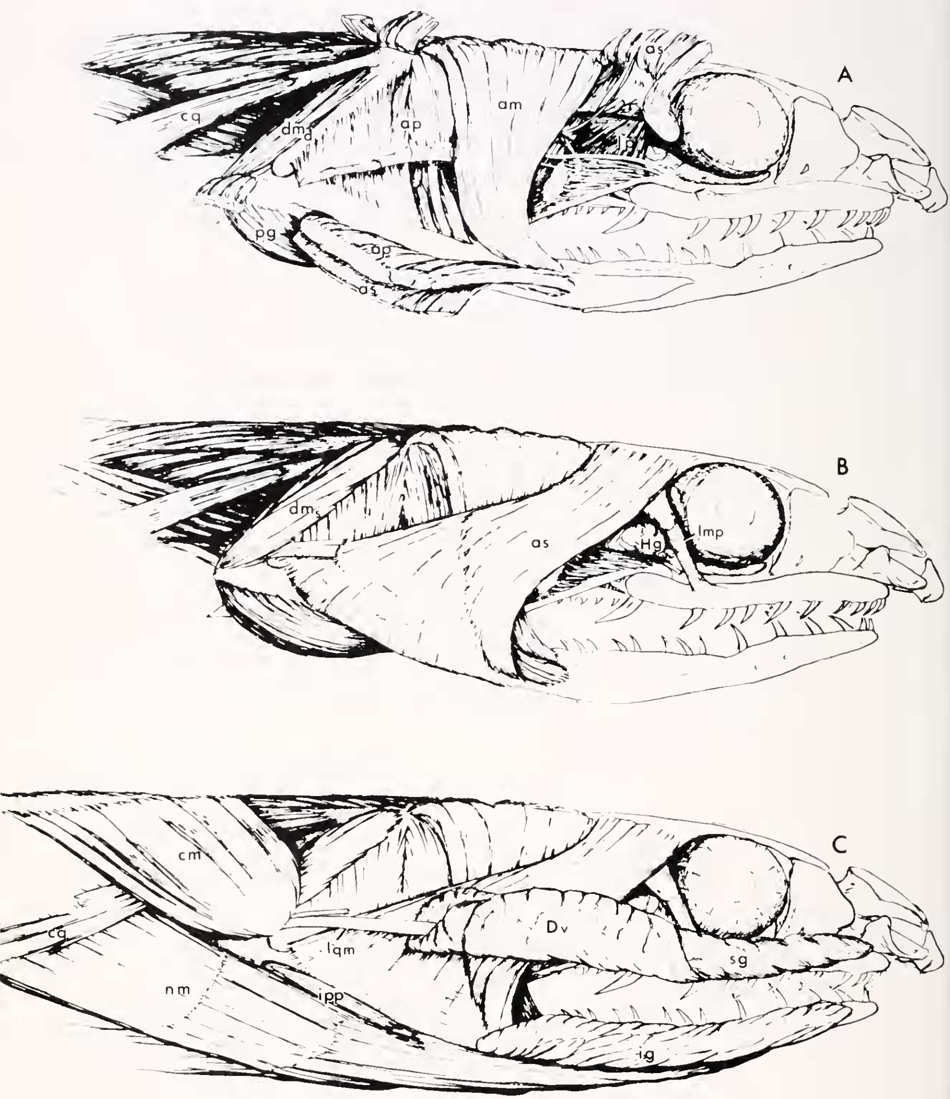
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bulae externus medialis. Its anterior fibers arch around the corner of the mouth without forming any attachments to the buccal membrane and pass to the mandible, where they directly insert on the compound bone just posterior to the end of the dentary tooth row and lateral to the anterior insertion of the adductor mandibulae externus profundus. The remaining fibers of this flat muscle terminate superficial to the profundus in a broad aponeurosis that spreads across the surface epimysium of the profundus and can be followed to an insertion extending in a narrow line from the lateral epicondyle of the quadrate along the mandible, ventral to the insertion of the profundus, and forward to a point not quite reaching the directly inserting anterior fibers described above.

M. adductor mandibulae externus profundus (ap)
Figs. 1, 3 c–d, 4 a–c

This is a large, triangular block of muscle divisible into two muscle wedges that separate cleanly along a vertical cleft between them. The anterior wedge takes origin from the lateral, anterodorsal corner of the quadrate. The origin of the posterior wedge also begins on this corner of the quadrate beneath the attachment of the anterior wedge. However, the origin of the posterior wedge extends

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Figure 4. Lateral view of skull showing progressively (A–C) more structures in place.

Abbreviations:

am	M. adductor mandibulae externus medialis
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dm	M. depressor mandibulae, deep division (d), superficial division (s)
Dv	Duvernoy's gland
Hg	Harderian gland
ig	infralabial gland
ipp	M. intermandibularis posterior, pars posterior
lmp	ligmentum maxillo-postorbitale
lp	M. levator pterygoidei
lqm	ligamentum quadrato-maxillare
nm	M. neuromandibularis
pg	M. pterygoideus
sg	supralabial gland

distally along the anterolateral edge of the quadrate reaching the lateral epicondyle. Both parts form a large, thick muscle that inserts directly on the lateral side of the compound bone in a low depression from below the quadrato-mandibular articulation forward to the posterior infralabial nerve foramen.

M. adductor mandibulae externus medialis (am)
Figs. 1, 3 c–d, 4 a–c

This muscle takes origin from the parieto-supratemporal ligament and the posterior half of the temporal crest, filling a depression and area adjacent to the crest. As the muscle passes ventrally its fibers gather into two divisions—superficial and deep. Dorsally a few fibers intermingle between both but as they pass downward they become more discrete. The deep division takes origin along the posterior temporal crest only. This division descends as a wide, thin sheet that inserts directly to the compound bone medial to the adductor mandibulae posterior. This insertion then extends forward and upward to the dorsal edge of the compound bone reaching a point posterior to the end of the dentary tooth row. The superficial division contains most of the fibers of this muscle and originates from both the posterior temporal crest and the parieto-supratemporal ligament. It narrows and gives rise to a short tendon that inserts on the dorsal, posterior end of the dentary.

M. adductor mandibulae posterior (apo)
Figs. 1, 3 c–d

This muscle, composed of parallel fibers, is triangular in shape and concealed beneath the adductor mandibulae externus profundus. It passes to both sides of the prearticular crest and so is divided naturally into two major parts—lateral and medial. In addition, a distinctive broad, flat muscle sheet forms the most lateral division, here referred to as the pars minimus.

The pars minimus takes origin at the base of the proximal end of the quadrate and then extends along its entire anterior, lateral edge to a point above the lateral condyle. It inserts along the dorsal edge of the surangular crest forward to a point just posterior to the adjacent mandibular nerve. The lateral division of the muscle takes origin along the anteromedial length of the quadrate. Its parallel fibers pass ventrally and forward to insert directly on the floor of the mandibular fossa and lateral side of the prearticular crest.

The medial division of this muscle takes origin along the medial side of the quadrate but more posterior in position than the lateral division. A few central fibers arise from a small, short, common tendon, but most are parallel and all collectively form a sheet that passes in an anteroventral direction eventually inserting directly on the dorsal edge of the prearticular crest and along a low depression on its medial face. The anterior part of this insertion passes lateral to the posterior insertion of the deep division of adductor mandibulae externus medialis.

M. pseudotemporalis (pst)
Figs. 1, 3 b–d

This muscle arises beneath the anterior part of the adductor mandibulae externus medialis and the posterior part of the adductor mandibulae externus superficialis along the mid-temporal crest. It is a ribbon-like muscle of parallel fibers that courses ventrally, passing deep to the maxillary division of the trigeminal (V) nerve, the facial carotid artery, and jugular vein. It attaches directly to the compound bone medial and slightly anterior to the front of the deep division of the adductor mandibulae externus medialis.

M. pterygoideus (pg)
Figs. 1, 2, 3 c–d, 4 a–b, 5 a–b

The pterygoideus takes origin from the lateral maxillary process of the ectopterygoid, primarily by a prominent tendon. The tendon remains superficial and passes ventrally reaching the middle of the muscle. Most muscle fibers arise along the length of this prominent tendon although a few directly arise from a small area on the ectopterygoid immediately medial to the origin of this tendon. The fibers sweep backward forming, on approach to the insertion, the swollen belly of the muscle that projects below the compound bone. The fibers curve upward to insert on the ventral surface of the mandibular retroarticular process. Specifically, this insertion includes the ventroposterior surface of the retroarticular process and extends a short distance forward along the ventrolateral edge of the process to a point even with the articular notch.

There are two further noteworthy anatomical features of this muscle. First, along its anterolateral surface the epimysium is drawn up into a loose fascial connection that joins it with the anterior edge

of the nearby adductor mandibulae externus medialis. Second, fibers composing the anterodorsal part of the muscle form a separate fascicle. Though anatomically an integral part of the pterygoideus, these fibers insert, via a wide aponeurosis, on the ventrolateral edge of the retroarticular process. Most fibers of this slip arise directly from the prominent ventral tendon near its anterior end, but a few arise directly from the lateral maxillary process of the ectopterygoid medial to this tendon.

M. pterygoideus accessorius (pga)
Figs. 1, 2, 3b

This muscle arises directly from the ventral surface of the pterygoid and base of the ectopterygoid. Specifically, this origin includes the ventral surface of the lateral projection of the pterygoid, its lateroventral groove, and lateroposterior base of the ectopterygoid. The muscle passes backward to insert on the inner side of the retroarticular process along its medial curvature, parallel with but medial to the insertion of the pterygoideus.

M. protractor quadrati (pq)
Figs. 2, 3 a–b

This muscle arises from a tendon, shared with its contralateral partner, that originates from the midventral basioccipital. It is a flat muscle, passing horizontally in a posterolateral direction over the dorsal surface of the protractor pterygoidei. A few fibers insert on the medial epicondyle of the quadrate, but most insert directly to the dorsomedial side of the mandibular retroarticular process, dorsal to the origin of the pterygoideus accessorius.

M. protractor pterygoidei (pp)
Figs. 1, 2, 3b

This muscle takes origin from the basisphenoid, specifically from a mid-transverse ridge, and forward parasagittally along the basisphenoid to a point just past the anterior Vidian foramen. It passes posteriorly, becoming fusiform in shape, and inserts across the posterodorsal end of the pterygoid with an especially firm attachment to the caudal tip of the bone.

M. levator pterygoidei (lp)
Figs. 1, 2, 3 a–d, 4a

A low depression in the posterior, ventral face of the postorbital process of the parietal serves as the surface from which this muscle takes origin. It passes ventrally, widening along an anteroposterior axis to form a long insertion on the pterygoid. This insertion begins posteriorly on the dorsolateral side of the pterygoid, runs forward to the ectopterygoid-pterygoid articulation, across the base of the ectopterygoid, and ends on the adjacent outer side of the pterygoid short of the pterygo-palatine articulation. The insertion thus lies along the shaft of this bone occupying the dorsolateral fossa.

M. retractor pterygoidei (rp)
Fig. 2

This muscle arises directly from the anterior slope of the transverse ridge on the basisphenoid, adjacent to the origin of the protractor pterygoidei. It passes forward to insert directly on the anterodorsal surface of the pterygoid and posterodorsal surface of the palatine, and by a broad aponeurosis to the posterior edge of the choanal process of the palatine.

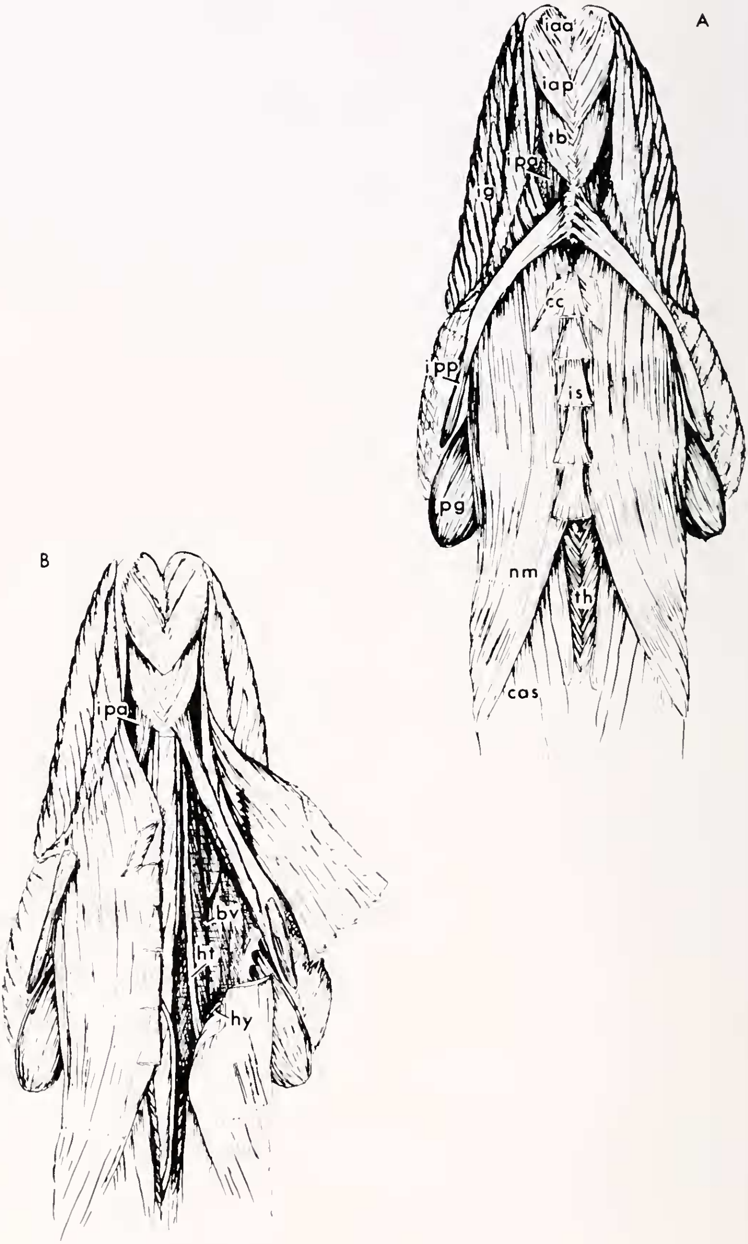
M. retractor vomeris (rv)
Fig. 2

This muscle arises from the sphenoid, lateral to the anterior end of the origin of the protractor pterygoidei. It passes forward as a spindle-like muscle bounded laterally by the retractor pterygoidei. Anteriorly, its fibers converge into a slender cord-like tendon that accounts for half the total muscle length. This tendon inserts on posterodorsal corner of the vomer.

Throat Musculature

M. neuromandibularis (nm)
Figs. 1, 4c, 5 a–b, 6b

Beginning in the neck, this broad, flat muscle sweeps downward and forward around the side of the body, passing under the cervicoquadratus and over the axial musculature, to insert at several sites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along the mandible via aponeuroses. It has been variously treated by other authors, some dividing it into several parts (Langebartel, 1968; Kardong, 1973; Haas, 1973) while others include it as part of a composite muscle (Albright and Nelson, 1959; Cundall, 1974). For descriptive purposes, it is here treated as a single unit. It originates from the epimysium of the spinalis-semispinalis muscles adjacent to neural spines 6–11. The anterior part of this origin lies under the posterior part of the cervicomandibularis. As it passes into the throat, it is crossed by two inscriptions. A separate muscle, the costomandibularis arises by three separate slips from the ventrolateral tips and costal cartilages of ribs 2–4. From here the costomandibularis passes forward to join and most fibers terminate on the medial face of neuromandibularis along the posterior inscription. Farther anteriorly, the neuromandibularis is joined by a few additional fibers originating from the lingual process and anterior end of the ceratobranchial of the hyoid; these fibers contribute to the medial border of the muscle.

Insertion on the mandible is by a broad aponeurosis, but along three specific sites. One site of insertion, via an aponeurosis, is along the ventral edge of the angular and posteroventral edge of the splenial. A second insertion, also via an aponeurosis, begins along the posterolateral edge of the dentary where it articulates with the com-

Figure 5. Ventral view of throat musculature. At bottom (B), a section of each intermandibularis posterior, pars posterior (ipp) has been removed. The left neuromandibularis (nm) has been cut and reflected to expose the underlying structures, including a prominent blood vessel (bv).

Abbreviations:

cc	M. constrictor colli
cos	M. costomandibularis
ht	M. hyotrachealis
hy	hyoid
iaa	M. intermandibularis anterior, pars anterior
iag	M. intermandibularis anterior, pars glandularis
iap	M. intermandibularis anterior, pars posterior
ig	infralabial gland
is	M. interscutali
ipa	M. intermandibularis posterior, pars anterior
ipp	M. intermandibularis posterior, pars posterior
nm	M. neuromandibularis
tb	M. transversus branchialis
th	M. transversus hyoideus

pound bone. This insertion extends forward along the lateral face of the dentary, passing below the anterior mental foramen and terminates behind the intermandibularis anterior. Thirdly, the epimysium along the superior face of the neuromandibularis forms an aponeurosis that passes dorsal to the origin of intermandibularis posterior, pars anterior to insert adjacent to it on the mandible. This forms a sleeve through which intermandibularis posterior, pars anterior passes from its origin forward toward its insertion (5b, 6b).

M. intermandibularis posterior (ipa, ipp)
Figs. 1, 4c, 5 a–b, 6b

The intermandibularis posterior, pars posterior takes origin beneath the insertions of the adductores mandibulae profundus and superficialis along the ventral surface of the compound bone. It is a strap-like muscle that passes forward superficial to the neuromandibularis to join its contralateral partner in inserting in the dermis at the central midline, just posterior to the origin of transversus branchialis.

The origin of intermandibularis posterior, pars anterior is also along the ventral edge of the mandible, but anterior to the insertion of the pars posterior. Forming into a strap-like muscle, it passes through a sleeve formed by the insertion of the neuromandibularis and then runs medial to the mandibular ramus. It inserts in the posteroventral epimysium of the transversus branchialis.

M. intermandibularis anterior (iaa, iap, iag)
Figs, 1, 5 a–b, 6 a–b

The muscle originates from the anteroventral tip of the dentary as the bone narrows and bends inward. This is lateral to the origins of the genioglossus and geniotrachealis. Though not anatomically separate, two regions of this muscle can be recognized—an anterior region (pars anterior), whose fibers pass inward to insert on the interramal pad, and a posterior region (pars posterior), that also passes inward to insert in dermis with its contralateral partner on a midventral raphé.

Anterior fibers of the intermandibularis anterior, pars glandularis (=constrictor of Langebartel, 1968) are fan-shaped and attach to the lateral edge of the interramal pad. The narrow posterior part of the muscle wraps around the ventral aspect of the lateral sublingual gland and attaches along the posteroventral surface of this gland.

M. transversus branchialis (tb)
Figs. 5 a–b, 6 a–b

This muscle originates from two heads, glandular and mucosal (pars glandularis and pars mucosalis respectively, of Albright and Nelson, 1959). The glandular head arises on the posterior end of the lateral sublingual gland. It passes as a ribbon-like band, arching posteriorly around the more medial genioglossus and geniotrachealis, then ventromedially to form the anterior part of the muscle. It is joined by fibers of the mucosal head arising from the dermis of the buccal epithelium midway between mandible and trachea to form the middle and posterior parts of the muscle. It inserts in the dermis of the chin integument at the ventral midline, between insertions of intermandibulares anterior and posterior.

M. genioglossus (gg)
Figs. 1, 6 a–b

Posteriorly this paired muscle is entwined around the tongue. Anteriorly, it originates from two heads. The medial head arises from the posterior tip of the interramal pad, then passes caudally around the lateral face of the medial sublingual gland.

The lateral head receives a few fibers from the dorsal surface of the intermandibularis anterior, but most arise from the anterior tip of the dentary along its inward inflection ventral to the geniotrachealis and dorsal to the intermandibularis anterior. It slants inward as a narrow cord-like muscle to join with the medial head near the middle of the medial sublingual gland. Just posterior to this gland, the muscle passes to the tongue sheath along which it runs caudally. About half way along the tongue, right and left genioglossus muscles change sides. The right muscle passes across the ventral surface to the left side and, at the same point, the left muscle passes across the dorsal surface to the right side. They stay in these reversed positions until reaching their posterior insertions on the hyoglossus, at the point of termination of the tongue sheath.

M. geniotrachealis (gt)
Figs. 1, 5b, 6 a–b

This muscle inserts along the side of the trachea beginning just posterior to the intrinsic laryngeal musculature (Kardong, 1972) spanning 9 cartilaginous rings. It passes forward as a ribbon-like

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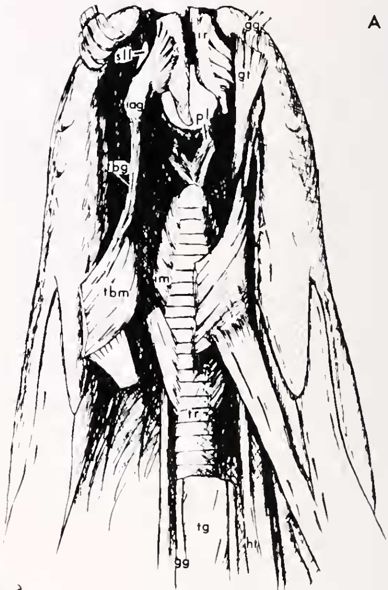
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